Early transition in foraging mode promoted greater reproductive effort in widely foraging lizards

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Abstract

Life-history theory predicts that the optimal reproductive effort of an organism is affected by factors such as energy acquisition and predation risk. Although this is a major focus of study in evolutionary ecology, the empirical evidence consists of conflicting data on a few organisms. For instance, theoretical models within the foraging mode paradigm suggest that widely foraging females have evolved low reproductive effort, because a heavy reproductive load decreases their ability to escape from predators. By contrast, a long-standing prediction of evolutionary theory indicates that organisms subject to high mortality due to predation, as suggested for widely foraging species, should increase their reproductive investment. Here, we revise the available literature on the relationship between foraging mode and reproductive effort of lizards. In doing so, we present evidence that widely foraging species have evolved greater reproductive effort than sit-and wait species. This is the largest comparative analysis of foraging mode and reproductive effort to date: 485 species grouped in 32 families. Based on our findings, we propose a theoretical model derived from the optimal foraging theory that potentially explains the observed patterns in lizards, paving the way for ecologist to test mechanistic hypotheses at the intraspecific level.

Main Text

Introduction

The foraging behaviors of vertebrates lie along a continuum, ranging from the energetically demanding strategy of foraging actively to the energetically conservative strategy of sit-and-wait foraging (Pianka 1966; Perry 1999). Over the past 50 years, ecologists have developed a set of hypotheses about how an organism's foraging mode relates to its life history (Vitt & Congdont 1978; Vitt & Price 1982; Dunham *et al.* 1988; Webb *et al.* 2003). These relationships stem from two major assumptions (Fig. 1). First, widely foraging animals spend more energy to forage than a sit-and-wait foragers, but might also consume enough food to have more surplus energy (Anderson & Karasov 1981, 1988; Huey & Pianka 1981; Nagy *et al.* 1984; Stuginski *et al.* 2018; Bury 2021). However, sit-and-wait foragers might exhibit wider diet breadths, because they encounter prey less frequently compared to active foragers (Glaudas *et al.* 2019). Second, a widely foraging animal could suffer a greater risk of mortality because its movements are conspicuous to predators (Cooper & Perez-Mellado 2004). Both a greater energy supply and a greater mortality risk would select for genotypes that allocate more energy to reproduction, manifested as more or larger offspring (Bonnet *et al.* 2001; Silva *et al.* 2020). The evolution of greater reproductive effort could feed back on the energy gain and mortality risk if a female carrying a greater mass of offspring tends to chase prey (Shine 1980). Similarly, the load associated with food consumption may compromise the locomotion of individuals, increasing the vulnerability to predators (Werner & Anholt 1993; Cooper 2000). In this model, a suite of traits associated with foraging mode would coadapt to the spatiotemporal distributions of prey and predators.

Despite the wealth of conjecture, these hypothetical relationships among foraging mode and other traits have been assessed in only a handful of cases, as described above. Ideally, one would isolate each relationship and conduct experiments to quantify the evolution of traits in

controlled environments (Huey & Bennet 1986). However, such data are difficult to gather for many species and will probably remain rare. For instance, limited circumstantial evidence exists for the putative relationship between foraging mode and predation risk. Data on stomach contents of field-collected vipers suggested that widely foraging lacertids are more vulnerable to predators than sedentary species (Huey & Pianka 1981), but a number of confounding factors can explain this observation as well as foraging mode can. Alternatively, researchers have evaluated the relationship between mortality and life-history traits with no emphasis on foraging behavior. For example, experimental evolution with guppies and fruit flies revealed that genotypes that evolved in risky environments developed more rapidly, matured at a smaller size, and reached their peak of fecundity faster than did genotypes that evolved in safe environments (Stearns 2000; Reznick *et al.* 2001). From these results, we expect that a high rate of predation selects for greater reproductive effort, but given the scarce evidence, it is still uncertain whether foraging mode generally affects predation risk or net energy gain.

Although experimental data are lacking, comparative methods have been used to explore how foraging mode and life-history traits have evolved. These interspecific analyses have focused mostly on the reproductive effort of lizards. The earliest analysis of 22 species revealed an unexpected pattern: sit-and-wait species had a greater reproductive effort than widely foraging species (Vitt & Congdont 1978). The authors suggested that widely foraging species might be forced to carry fewer or smaller offspring, because moving long distances with a voluminous clutch decreases the chance of escaping from a predator. A subsequent analysis of data for 50 species of lizards supports this result by testing a model in which predation risk increased with increasing reproductive effort (Vitt & Price 1982). Consecutively, Roff (2002) extended support for this model in a comparative analysis of 130 lizard species. However, none of these early analyses controlled for potential phylogenetic correlations that might generate spurious relationships between foraging mode and reproductive effort (Felsenstein 1985), especially because foraging could vary greatly among but little within families. A more recent analysis, using

phylogenetic comparative methods, failed to detect a significant relationship between foraging mode and reproductive effort (Mesquita *et al.* 2016). Thus, despite several attempts to establish a relationship between foraging mode and the life history, we still lack support for a long-standing prediction of the foraging-mode paradigm.

Here, we present the first evidence that widely foraging species have evolved greater reproductive effort than sit-and wait species. This evidence comes from the largest comparative analysis of foraging mode and reproductive effort to date: 485 species of lizards representing 32 families. In this analysis, we inferred the evolutionary history of foraging modes, complementing on past reconstructions of ancestral states (Miles *et al.* 2007). In contrast to previous analyses, our study supports the prediction of theoretical models of the optimal reproductive effort, paving the way for ecologists to test mechanistic hypotheses at the intraspecific level.

Materials and Methods

Data source and description of variables

We used published estimates of life history and foraging behavior for 485 species of lizards grouped in 32 families, excluding amphisbaenians and snakes. These data represent a subset of a data assembled from primary and secondary literature on lizards' traits published during the last 12 years (Meiri 2018). The reproductive effort of the species was defined as the product of the mean snout-vent length of hatchlings or neonates (mm) and the mean clutch or litter size. Given the limited data available for clutch frequency in widely foraging and sit-and-wait species, we could not examine the lifetime reproductive effort of lizards. Instead, our measure represents the investment of females in a single reproductive event. Our measure of maternal size consisted of the mean snout-vent length of adult females. We used the length of hatchlings rather than the mass of eggs, because the latter might reflect high water content rather than energy content in

lizards that lay poorly calcified eggs (Deeming 2004; Meiri *et al.* 2015). Moreover, hatchling size can be measured for viviparous species as well as oviparous species.

Although relative clutch mass is commonly reported as an index of reproductive effort, we used a different index to avoid statistical issues associated with analyzing a ratio. Ratios of random numbers regressed against their denominator will automatically yield negative correlations (Atchley *et al.* 1876; Packard & Boardman 1988). For example, a comparative study of 551 species of lizards revealed a negative effect of maternal size on relative clutch mass (Meiri *et al.* 2012). This result is difficult to interpret as it contrasts with most theoretical models, which predict that relative clutch mass should increase with maternal size (Roff 2002)—a pattern observed in many organisms (e.g., Primack 1979; Barneche et al. 2018; Marshall et al. 2021).

We defined the foraging mode of a species based on whether it has been reported as an ambush predator ("sit-and-wait"), an active forager ("widely foraging"), or uses a mixed strategy ("mixed"). Although this categorization seems somewhat artificial and simplistic, numerous species of lizards clearly belong to one of these categories (Huey & Pianka 1981; Perry 1999). We focused our analyses only on carnivores, because herbivores do not fit into the classical paradigm of foraging modes (Pianka & Vitt 2003).

Ancestral character and phylogenetic signal estimates

To determine the appropriate model of evolution, we used a set of continuous-time discrete-state Markov chain models to sample the character histories from their posterior probability distribution (Huelsenbeck *et al.* 2003), and a time-calibrated phylogeny of squamate reptiles (Zheng & Wiens 2016). We rooted the tree with the Tuatara (*Sphenodon punctatus*) as the outgroup for our study taxa. Based on previous analyses, we coded this outgroup as a sit-and-wait forager (Pianka & Vitt 2003; Vitt *et al.* 2003). We fitted three different models to our data, using the function *make.simmap* from the R package "phytools" version 0.7.80 (Revell 2012; R Core Team 2021).

These models were as follows: 1) an equal rates model (ER), in which the rate of change between all three states of the character are assumed to be equivalent; 2) an all-rates-different model (ARD), which allows the transitions among states to have different rates; 3) and a symmetrical model (SYM), which allows different rates of change between pairs of states but changes between all states are theoretically possible. For each model, we estimated the stationary distribution by numerical solving for *pi* (*pi* = 'estimated'), and this was used as prior distribution on the root node of the tree. These models sample the character histories conditioned on the transition matrix (Q matrix) and use the phylogenetic tree with annotated tips to create stochastic simulation maps for the potential evolutionary transitions between foraging modes. To describe the variation in reproductive effort across the study taxa, we plotted bars adjacent to the tips of the phylogeny representing values of species reproductive effort. We selected the most likely model of evolution based on the Akaike Information Criterion (AIC). Lastly, we generated 10000 trees of the most-likely model and used the *summary* function to count the total number of transitions that occurred between character states (see supporting material for detailed information).

We computed our measure of phylogenetic signal (or character dispersion on a phylogeny) by using the Fritz and Purvis' $D\ test$, available through the function *phylo.d* in the R package "caper" version 1.0.1 (Fritz & Purvis 2010; Orme *et al.* 2018; R Core Team 2021). This parameter is calculated as follows:

$$D = \frac{[\sum d_{obs} - mean(\sum d_b)]}{[mean(\sum d_r) - mean(\sum d_b)]},$$

where d_{obs} equals the number of character-state changes required to get the observed distribution of character states at the tips of the phylogeny. The d_{obs} is then scaled using two null distributions. The first distribution, d_r, comprises d values obtained from permutations where the

number of species with each character state is kept constant, but the values are shuffled on the tips of the phylogeny. Thus, $d_r$is the expected distribution of d values if character states are randomly distributed among species without respect to phylogeny. The second distribution, d_b, comprises the d values expected if character states are distributed among species under the expectations of the Brownian motion model of evolution. We generated d_b by simulating a continuous trait along the phylogeny, then defining the character state at each tip according to some threshold value of the continuous trait (Fritz & Purvis 2010). The value of D equals 1 if the distribution of the binary trait is random with respect to phylogeny, and exceeds 1 if the distribution of the trait is more overdispersed than the random expectation. The value of D equals 0 if the binary trait is distributed as expected under the Brownian motion model of evolution, and is less than 0 if the binary trait is more phylogenetically conserved than the Brownian expectation. The distributions d_r and d_b were used to assign $p - values$ to d_{obs}. Accordingly, if d_{obs} is larger than 95% of d_r values, the distribution of the trait would be significantly more overdispersed than the random expectation, if d_{obs} is less than 95% of d_b values, the character would be significantly more clumped than the Brownian expectation.

Effects of body length and foraging mode on reproductive effort

We fitted Phylogenetic Generalized Least Squares models (PGLS) to test our prediction on the relationship among body length, foraging mode, and the reproductive effort of lizards. In comparative biology, normal regression models cannot be used because the assumption of independence of residuals is violated (Felsenstein 1985; Harvey & Pagel 1991). This problem can be corrected using phylogenetic comparative methods. We fitted the models using the function *gls* from the R package “nlme” version 3.1-152 (Pinheiro *et al.* 2021; R Core Team 2021). We adopted the reproductive effort of lizards as our response variable. Similarly, maternal length and foraging mode corresponded to our predictor variables. We fitted the models assuming two ways in which the tree structure was expected to affect the covariance in trait values across taxa (corBrownian and corPagel —value = 0— error structures, using the R package “ape”). We

selected the best-fit model based on the AIC values (see supporting material for detailed information). To avoid confounding results due to a potential large variation in maternal length among species, we not only tested our prediction for all lizards in our data set (Fig. 3A), but also examined the data at lower taxonomic scales (e.g., within the superfamily Scincoidea; Fig. 3B). Analyzing the data at different taxonomic scales enabled us to better investigate the level of support for the prediction tested.

Results

The evolutionary transitions in foraging modes among lizards were best described by a model in which rates of evolution differ among modes, referred to as the all-rates-different model. Despite a slightly difference with the widely foraging state, our analysis revealed that sit-and-wait foraging is the most likely ancestral state of all lacertilians (Fig. 2). Sit-and-wait foraging has evolved in two major clades of lizards; near the root of the tree, we found strong evidence suggesting that the ancestor of Gekkota was a sit-and-wait predator. Likewise, the ancestor of iguanians was a sit-and-wait predator. Iguanians included in our analysis are part of both the Acrodonta and Pleurodonta clades. During the early Jurassic (≈ 200 mya), a major transition from sit-and-wait to widely foraging occurred in the ancestor of Anguimorpha, Lacertoidea, and Scincoidea. Since then, a reverse transition from widely foraging to sit-and-wait foraging occurred within Scincoidea, in the ancestor of spiny-tailed lizards and night lizards (Cordylidae and Xantusiidae). The estimate of the $D\ test$ for phylogenetic signal indicated that foraging mode is phylogenetically conserved as expected under a Brownian motion model of evolution ($D = -0.14,\ p[D < 1] = 0,$ $p[D > 0] = 0.80$).

Our analyses show that widely foraging species have evolved greater reproductive effort than sit-and-wait species. However, the mechanism underlying this pattern is mediated by a complex interaction between foraging mode and maternal length (Table 1). In Lacertilia, widely

foraging species have greater reproductive effort for two reasons: 1) they are larger in size, and 2) on average, they give birth to a higher number of offspring for a given size (Fig. 3A). In the superfamily Scincoidea, widely foraging species evolved greater reproductive effort despite having a smaller mean body length (Fig. 3B). Interestingly, skinks that adopt a mixed foraging behavior have also evolved greater reproductive effort than sit-and-wait skinks.

Discussion

Our results show that widely foraging species have evolved a greater reproductive effort than sit-and-wait species. Presumably, the ability of widely foraging lizards to harvest and assimilate more resources might explain this pattern. Studies on field metabolic rate of free-ranging lizards suggest that an average widely foraging species spends 32% more daily energy than a sit-and-wait lizard, but this extra energy expenditure is probably paid off with greater daily food consumption (Brown & Nagy 2007). Food consumption may play an important role in determining the reproductive effort of lizards in three ways: 1) it promotes follicular growth during the reproductive season; 2) in the long term, it increases energy stores to initiate reproduction (e.g., vitellogenesis). and 3) it may also reduce age at first reproduction. Consistent with these ideas, Bonnet and colleagues found that female vipers that had good body condition early in vitellogenesis produced large litters (Bonnet *et al.* 2001). Similarly, vipers that gained more mass during follicular growth produced larger offspring. Early reproduction gives offspring sufficient time to mature in the same year that they hatched, which enables them to participate as adults in the subsequent breeding season (Hahn & Tinkle 1965). Therefore, the foraging behavior of a widely foraging female can increase the amount of gametic resources gathered before and during each reproductive bout, potentially resulting in more energy to invest in reproduction.

Additionally, maternal size also plays an important role in determining the reproductive effort of lizards. Among many ectotherms and plants, a common pattern is that reproductive effort

increases with size (Tinkle 1967; Primack 1979; Bownds *et al.* 2010; Barneche *et al.* 2018; Marshall *et al.* 2018, 2021). This observation indicates that increased size might evolve by natural selection, because it increases the fitness of individuals. Interestingly, our results paint a more complex picture of the effect of body size on reproductive effort. We found that the relationship between maternal length and reproductive effort depends on foraging mode. The most complex form of relationship occurs when small widely-foraging females have a greater reproductive effort than large sit-and-wait females (Fig. 3B). A model of the evolution of optimal reproductive effort predicts this pattern (Parker & Begon 1986). This model suggests that the total energy accumulated for reproduction (m) depends on the time spent foraging (t) and maternal size. Assuming that females have the same foraging efficiency, smaller females would reach their maximum capacity to accumulate resources at lower values of m, producing fewer or smaller offspring than larger females (Fig. 4A). However, if a widely foraging female has a smaller body size but a higher foraging efficiency, she may have greater reproductive investment than a large sit-and-wait female (Fig. 4B). The same outcome should be observed if a widely foraging female is both a larger and more efficient forager than a sit-and-wait female (Fig. 4C). Furthermore, if widely foraging females are more efficient at foraging, they may have both a shorter foraging time and a reduced interclutch interval. Therefore, widely foraging females might not only produce larger or more offspring in a single clutch, but they might also increase the number of clutches throughout their lifetime.

Because the risk of predation presumably depends on the time spent foraging, individuals that require less time to accumulate the optimal amount of resources should incur a lower probability of death. Based on the theory of foraging by Schoener, the energy accumulated from foraging increases monotonically toward an asymptote (Schoener 1971). In such cases, the law of diminishing returns implies that foraging for twice as long would not result in twice the energetic return (Fig. 4B). Therefore, greater foraging efficiency (more energy gain per foraging time) should enable an organism to survive better in environments with high predation risk. Consistent

290 with this idea, a study on foraging efficiency (defined as ratio of metabolizable energy gained
291 while foraging to the energy spent while foraging) partially indicates that widely foraging lizards
292 spent less time foraging but grew larger than did sit-and-wait lizards (Nagy *et al.* 1984). Indeed,
293 our results show that widely foraging lizards are, on average, larger than sit-and-wait lizards (Fig.
294 3A). The ability of widely foraging species to rapidly outgrow a sit-and-wait species may also
295 enable them to outgrow the gape limitations of predators (Lynch 1980; Reznick & Endler 1982).
296 Furthermore, when competition for mates is crucial, the winner of a mating-contest between two
297 competitors is generally the larger individual (Roff 2002). Therefore, if body size is critical to
298 outperform predators and outcompete conspecifics, the optimal pattern may be to grow to the
299 maximal size that leads to the greatest reproductive effort.
300
301 The foraging mode paradigm is mostly focused on dichotomous variation, yet plastic
302 variation in foraging mode may drive the evolution of the reproductive effort in some species.
303 Recent studies have revealed that the foraging mode of an organism depends on the ecological
304 context, such as presence of predators, abundance of prey, or habitat degradation (Greef &
305 Whiting 2000; Hawlena & Perez-Mellado 2009; Wasiolka *et al.* 2009; Donihue 2016). Such
306 plasticity could precede rapid evolutionary change and local adaptation of the life history
307 (Richardson *et al.* 2014). Our results show a strong presence of species that adopt a mixed
308 foraging strategy in the superfamilies Anguimorpha, Gekkota, Iguania, and Scincoidea (Fig. 2).
309 Interestingly, these lizards have greater reproductive effort than do sit-and-wait lizards,
310 specifically for species of relative small size (Fig. 3B). Because mixed foraging species are often
311 exposed to a wide range of environments with different selective pressures, these species might
312 actively select habitats that maximize their reproductive effort, indirectly resulting in local
313 adaptation (Richardson *et al.* 2014). Our analysis, which provides the first evidence that a mixed
314 foraging strategy can lead to greater reproductive effort, should encourage others to address the
315 questions raised by this discovery.
316

Our study presents the first evidence that the early shift in foraging mode—from sit-and-wait to widely foraging—in the evolutionary history of lacertilians was accompanied by the evolution of a greater reproductive effort in most widely foraging species (Fig. 3). Based on the theory of optimal foraging, we propose a theoretical model that potentially helps to better understand the evolution of the optimal life-history strategy. This model is emphasized on a complex covariation between energy gain, maternal size, and foraging mode. Investigating how much energy an individual obtains from the environment is crucial in life-history analysis because the flux of energy within an organism not only determines its survival, but also whether it can engage in reproduction, a very evolutionarily important activity. Currently, analyses of the energetics of foraging modes stem from measures of a few species in short periods of a season. Such data overlook the physiological and ecological constraints of seasonality on some organisms. For example, widely foraging lizards in the Kalahari Desert consume more food during the summer, but stop eating during winter as they hibernate. By contrast, sit-and-wait lizards probably forage during both seasons as they remain active during winter (Huey *et al.* 2021). Evidence of this nature is still rare in the current literature, revealing the need for long-term studies on the energetics of foraging modes. Similarly, direct comparisons of mortality rates in widely foraging versus sit-and-wait species are required, as the existing data prevent us from making convincing conclusions on the relationship between foraging mode and vulnerability to predation. Finally, our study captured the effects of foraging plasticity on the evolution of the reproductive effort of lizards. Overall, lizards that adopt a mixed foraging strategy also have greater reproductive effort than do sit-and-wait species. This result suggests that foraging plasticity can result in differential reproductive effort and opens the question for future studies of whether the foraging efficiency and predation risk of each mode influence the evolution of fecundity in species that forage plastically.

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Figures and Tables

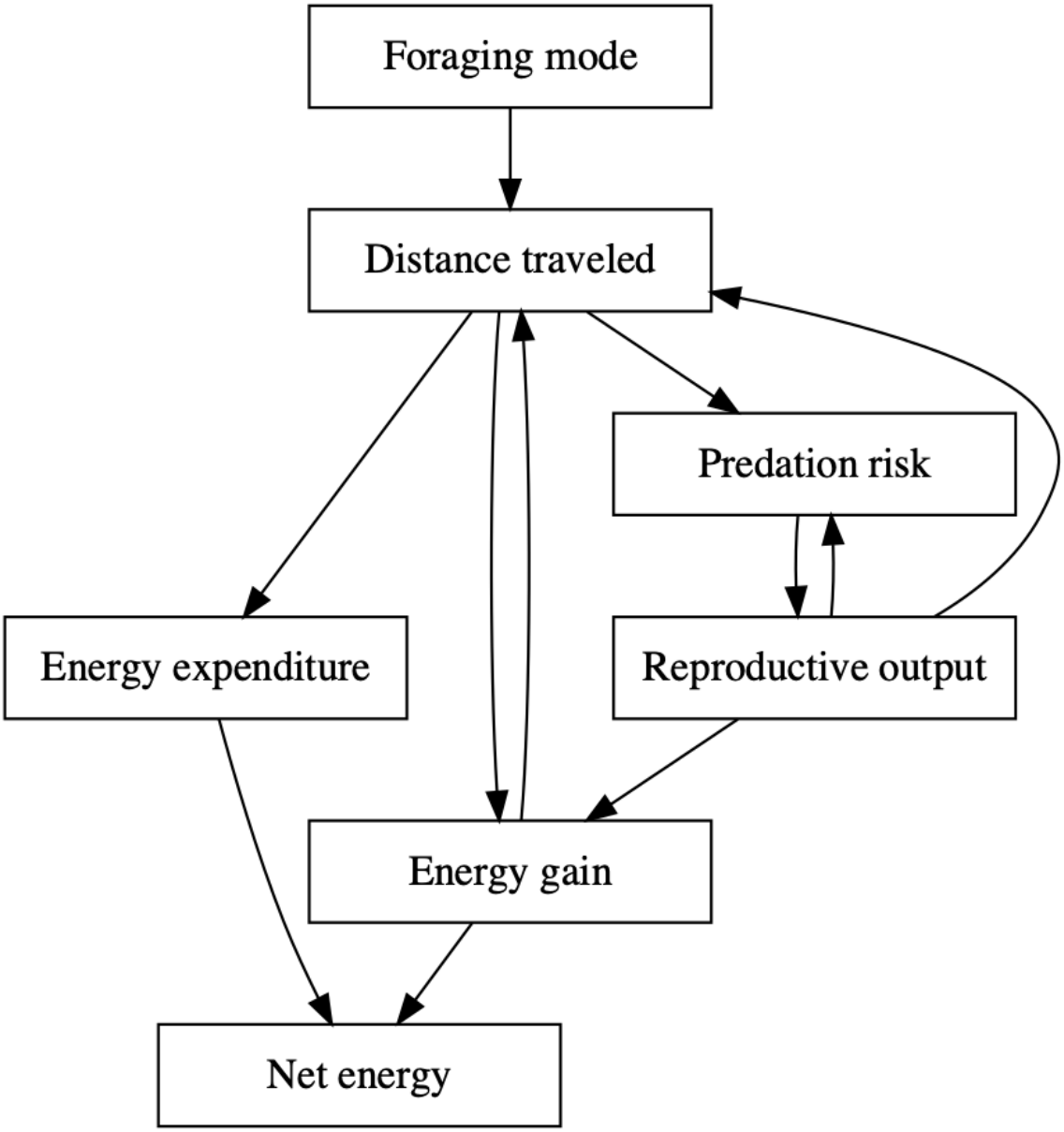

Fig. 1. Conceptual model depicting potential relationships between foraging behavior, energetics, predation risk, and reproductive effort. The predicted relationships derived from long-standing models of life-history theory (see text).

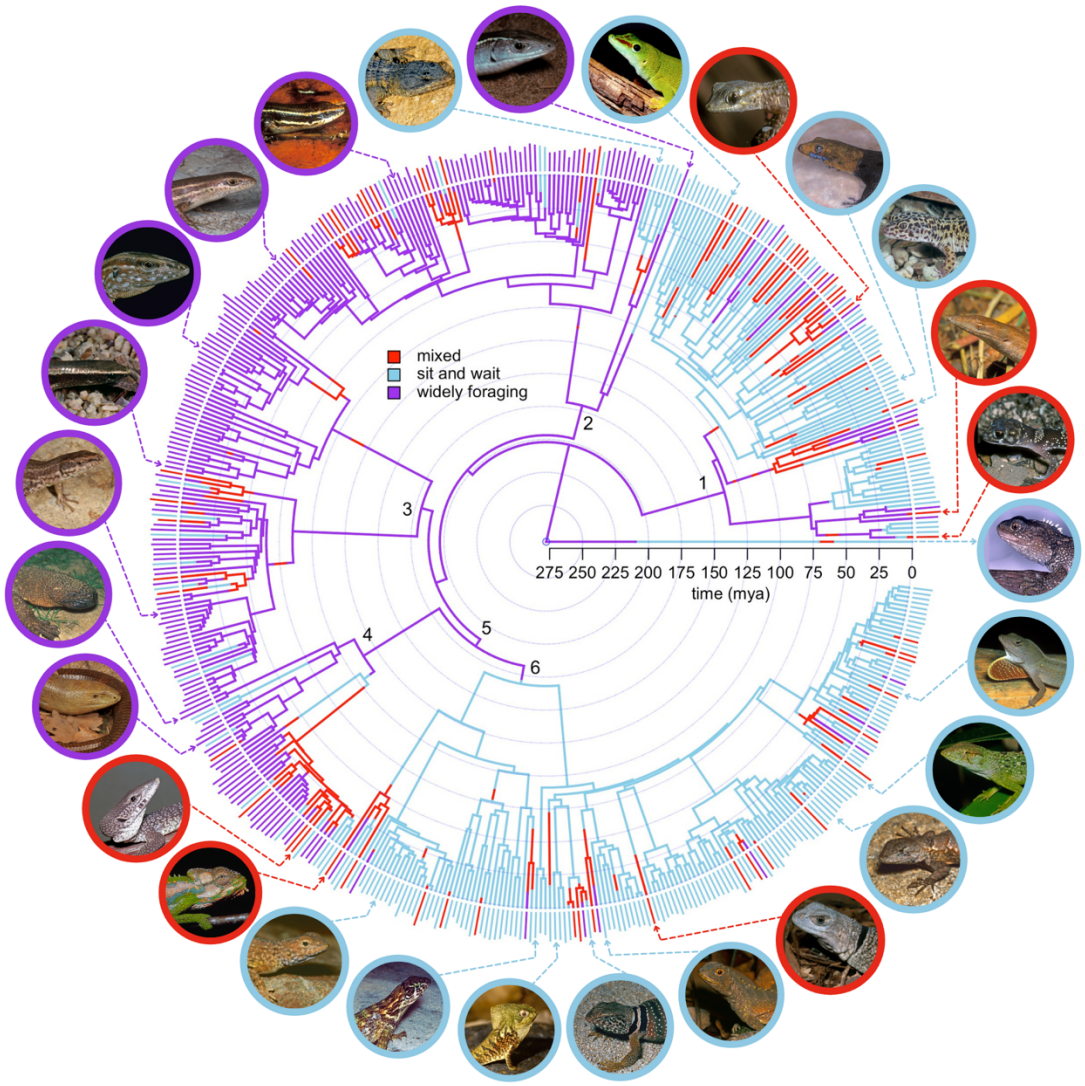

Fig. 2. Random sample of stochastic character maps depicting the evolution of foraging mode in 485 species of lizards (see supporting material for estimates of ancestral states in each internal node). Bars at the tips of the phylogeny represent log-transformed values of reproductive effort for all lizards, but not the outgroup *Sphenodon punctatus*. Major clades are enumerated as follows: 1) Gekkota, 2) Scincoidea, 3) Lacertoidea, 4) Anguimorpha, 5) Toxicofera, and 6) Iguania. Lizard photos by Mark O'Shea.

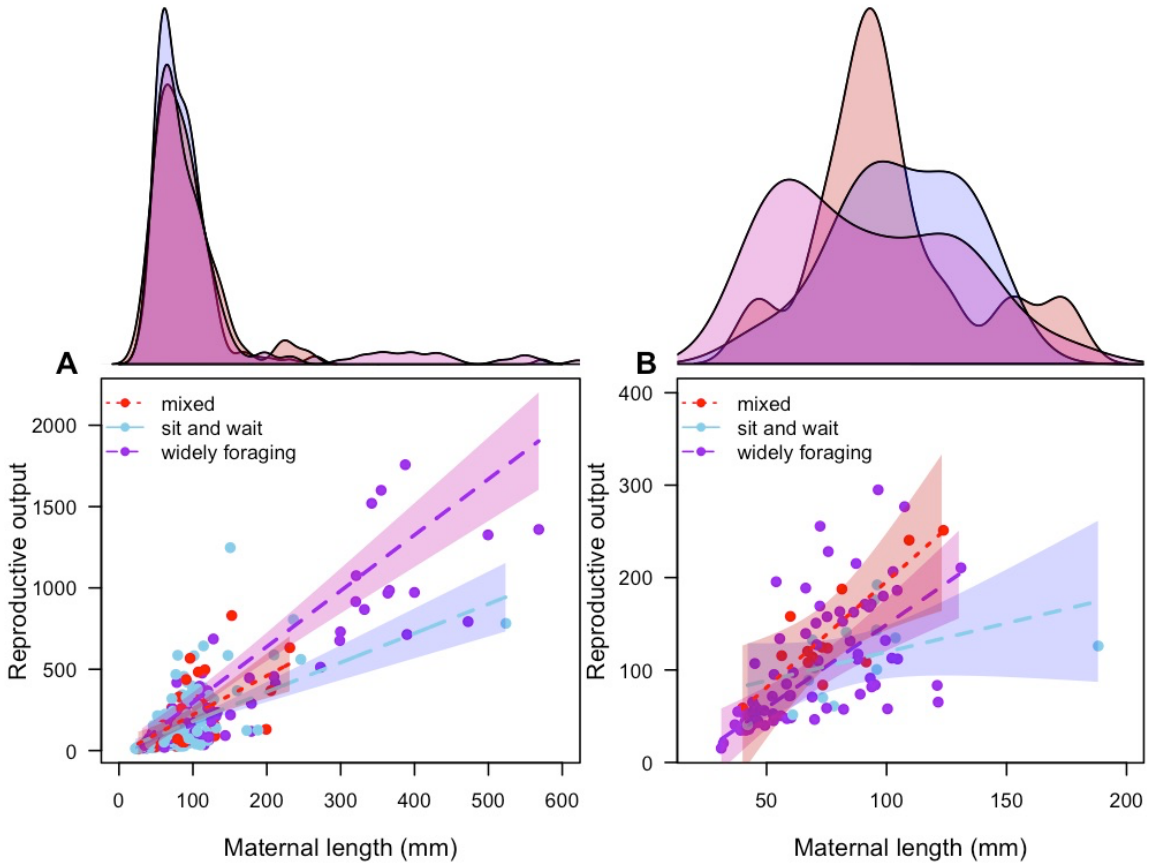

Fig. 3. Effects of maternal length and foraging mode on the evolution of the reproductive effort of lizards, as determined by phylogenetic generalized least squares analysis. A) In Lacertilians, widely foraging species have evolved the greatest reproductive effort. However, our analysis revealed a right-skewed distribution of body length in this clade. B) The same pattern holds in lizards with small and normal-distributed body length, such as skinks. According to the estimated parameters of the model, sit-and-wait species have the lowest reproductive effort ($\beta = -1.026, Std.Error = 0.507, t - value = -2.021, p = 0.046$).

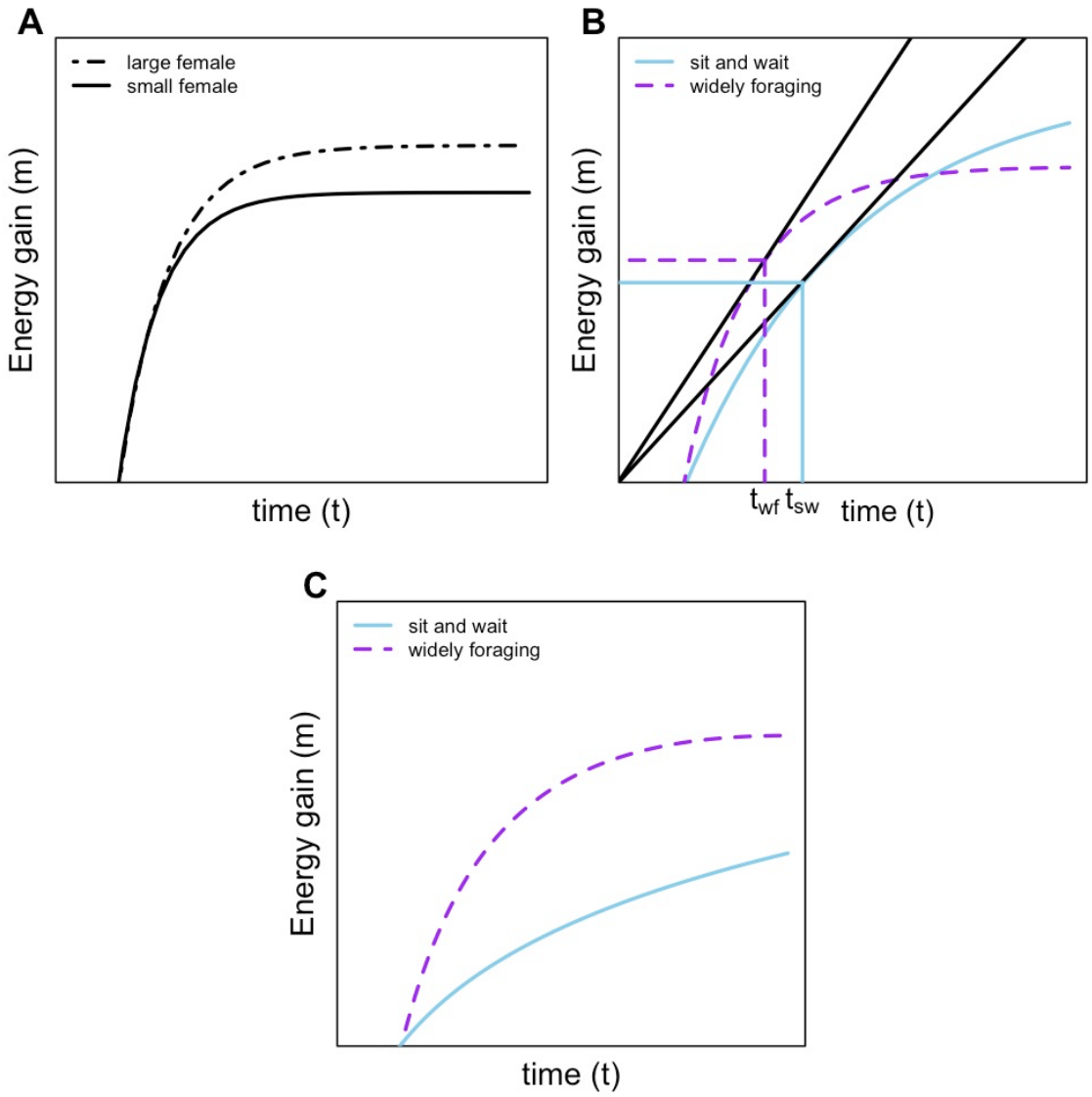

Fig. 4. Theoretical model relating the amount of energy gain for reproduction, *m*, as a function of time spent foraging, *t*, and maternal size. A) Larger females reach their maximum capacity at a higher value of *m* than small females. B) Widely foraging females that are smaller but more efficient foragers may produce a greater reproductive effort than larger sit-and-wait females. C) Widely foraging females may also produce a greater reproductive effort than sit-and-wait females if they are both larger and more efficient foragers. t_{wf} and t_{sw} in (B) represent the optimal foraging time of widely foraging females and sit-and-wait females, respectively.

Table 1. Summary statistics for the most likely model of evolution of the reproductive effort, based on the ranking of AICc for potential candidate models included in our analyses.

Terms	numDF	F-value	p-value
(Intercept)	1	27.560	<.0001
female.SVL	1	533.959	<.0001
foraging.mode	2	0.533	0.587
female.SVL:foraging.mode	2	19.910	<.0001